Lashley, Karl Spencer
Studies of cerebral
function in learning

BRAIN.

STUDIES OF CEREBRAL FUNCTION IN LEARNING.
No. III.—THE MOTOR AREAS.

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IN their first study of the electro-stimulable cortex of the dog, Fritsch and Hitzig [5] ascribed to it the function of control of voluntary movement, although they recognized that its destruction resulted in a difficulty rather than a complete loss of ability to make voluntary movements. The latter fact was largely disregarded by the investigators following them and the view that the fibres descending from the stimulable area form the chief efferent path from the cortex was adopted by Ferrier, Carville and Duret, Luciani, Bechterew, and other early workers, so that this theory has come to be accepted as one of the most firmly established facts of cerebral localization. From the first, however, certain facts, derived chiefly from studies of recovery from paralysis following lesion to the motor area, have seemed incompatible with this view. Fritsch and Hitzig emphasized the importance of other descending tracts, and Carville and Duret [4] showed that recovery from hemiplegia is not due to the vicarious functioning of the uninjured stimulable area. The belief that recovery from paralysis is only a revival of depressed reflex functions and that the power of voluntary movement is permanently abolished by complete destruction of the motor area was disproved by Rothmann [16] who observed the formation of motor habits in monkeys after destruction of the stimulable area of one hemisphere and the pyramidal and rubrospinal tracts of the opposite side.

Such experiments show that the extra-pyramidal fibres are capable of mediating complex activities of the habitual or voluntary type but

leave undecided the question whether this is their normal function or merely a vicarious function due to the destruction of the stimulable cortex.   In a previous study of the rôle of various parts of the cerebrum of the white rat in the formation and retention of visual habits the writer found that the habit of discrimination of light intensities survived the total destruction of the stimulable area.   Injury to an area on each occipital lobe corresponding to Brodmann's *area striata* [2] resulted in the complete loss of the visual habit, but any other third of the cortex might be destroyed without in the least disturbing the animal's ability to make the discrimination accurately.   The data reported in that study seem to prove that the conditioned-reflex arcs involved in visual habits descend from approximately the same area of the cerebral cortex to which they are projected and do not traverse the cortex to descend from the stimulable areas.   The visual habits have cerebral representation, but the supposed motor areas have no direct function in their performance [10].

In higher animals, especially the primates, complete paralysis of voluntary movement may follow destruction of the stimulable cortex, but this does not necessarily imply an interruption of the direct conditioned-reflex arcs.   Such an explanation is to be preferred on grounds of simplicity, if contradictory facts do not appear, but disturbances of some of the mechanisms of tonic reinforcement, not in the direct conditioned-reflex path (section of the afferent nerves of a limb, cerebellar injury, &c.), may produce somewhat similar disturbances of voluntary movement and indicate an alternative explanation of the function of the stimulable areas.   The demonstration that, in the rat, the stimulable area is not traversed by the conditioned-reflex arcs of visual habits seems sufficient evidence to raise the question of whether the so-called motor area is really a part of the mechanism for voluntary movement or is merely a part of the subsidiary tonic and postural mechanism.

Generalization from the rat to higher forms is complicated, however, by the probable transfer of function from the corpus striatum to the stimulable cortex, with ascent in the evolutionary scale.   In the rat, destruction of the stimulable areas produces no detectable motor disturbances, but simultaneous destruction of the motor area and the corpus striatum produces a paralysis which is relatively permanent and which resembles the effect of destruction of the stimulable area in higher forms [10].   This indicates that the function of the stimulable area of primates is represented in the rat by the combined function of

the stimulable area and the corpus striatum.[1]   In order that data obtained from the rat may be applicable to higher forms it is necessary, therefore, that both the stimulable cortex and the corpus striatum be considered.   My earlier study eliminated only the stimulable cortex from the habit mechanisms.   In the experiments reported below I have tested the effects of simultaneous destruction of the stimulable areas and the caudate portions of the corpora striata upon the rat's ability to form and retain visuo-motor habits.   The data outlined above make it fairly certain that in the combined lesion we are dealing with structures analogous in function to the stimulable areas of the primates and that conclusions valid for higher forms may be drawn from the experiments.

The chief question which the following experiments were designed to answer is, then, whether or not the structures of the rat's cerebrum, injury to which produces motor disorganization, are directly concerned in the performance of habitual acts.   Visuo-motor habits are best suited for such tests, since they are easily acquired and recognized.   A visual area in the occipital region is clearly defined and it has been shown that cortical representation of the habit is retained after 1,400 trials of overtraining [11], so that the possibility that the habits are carried out at subcortical levels is ruled out.

THE TOPOGRAPHY OF THE STIMULABLE AND VISUAL AREAS OF THE CEREBRUM AND OF THE CORPUS STRIATUM IN THE RAT.

The stimulable area in the rat includes the antero-dorsal third of the cerebral cortex.   It extends from above the anterior margin of the hippocampus forward to the frontal pole, covering the median half of the dorsal convexity in this region.   On the frontal pole it extends laterally and then caudally over the inferior orbital surface.   Fig. 1 shows a composite map of the area in about twenty-five animals, with the movements elicited by bipolar stimulation.   In the majority of animals the area does not extend so far caudally as in the diagram and only movements a, d, i, j, and p can be elicited.

The visual function seems limited to a small area on the dorsal

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[1] Since the pyramidal fibres are scattered throughout the caudate nucleus it is impossible to destroy the latter alone.   In earlier work [10] I found one case with extensive degeneration of the right caudate nucleus involving few of the pyramidal fibres and leaving the greater part of the stimulable area intact.   This animal showed an unusually rapid and complete recovery from the motor disturbances following operation and led to the tentative conclusion that the striate nucleus and stimulable cortex have interchangeable function.

convexity of the occipital pole.   Fig. 2 is a composite diagram of the lesions in nine animals in which habits of visual discrimination persisted after bilateral injury.   Detailed descriptions of these animals have been given in previous papers [10, 11].   In each animal the area destroyed included about one-fourth the blackened area of the diagram.   Fig. 3 is a composite diagram of the lesions in seven animals which lost the habit of visual discrimination after operation.   These two series of animals show clearly the restriction of cortical function in vision to the
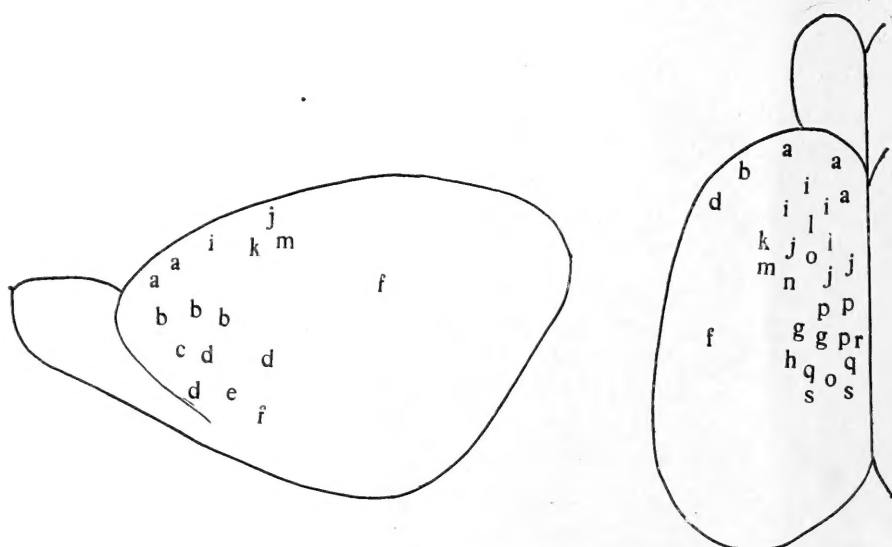

FIG. 1.—Composite diagram of the electro-stimulable points on the cerebral cortex of the rat. $a =$ Head turned to opposite side. $b =$ Nose retracted. $c =$ Vibrissæ moved. $d =$ Chewing movements, $e =$ Tongue protruded. $f =$ Eye closed. $g =$ Ear adducted. $h =$ Ear erected. $i =$ Shoulder drawn forward. $j =$ Fore-arm retracted. $k =$ Elbow flexed. $l =$ Elbow extended. $m =$ Wrist flexed. $n =$ Fore-arm rotated. $o =$ Back flexed to opposite side. $p =$ Hind leg drawn forward. $q =$ Homolateral leg flexed, ipselateral extended. $r =$ Ankle extended. $s =$ Tail drawn to opposite side. All movements are contralateral to the hemisphere stimulated, except where indicated.

occipital pole and the survival of the habit after destruction of the motor area.   The area included in fig. 3 corresponds roughly to Brodmann's *area striata* in other rodents [2].

The corpus striatum in the rat is very large in proportion to the volume of the cerebral cortex.   Fig. 4 shows it in frontal and horizontal sections through the levels used in later diagrams.   The caudate nucleus consists of masses of cells scattered among the fibres of the internal capsule and is nowhere distinct from the descending fibres. The lenticular portion is relatively free from pyramidal fibres.   The

experimental lesions described below are restricted to the caudate nucleus and this is also the part whose injury produces paralytic symptoms [10, 12].

EXPERIMENTAL METHODS.

Training.—For the study of visual habits a discrimination box of the type designed by Yerkes was used. It consists of a central compartment opening into two parallel alleys which lead by lateral passages
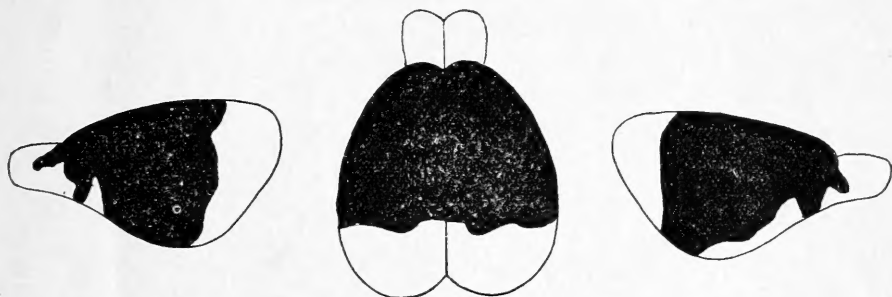

FIG. 2.—Composite diagram of the lesions in animals which retained the habit of visual discrimination after operation. The habit survived the destruction of any third of the blackened area.
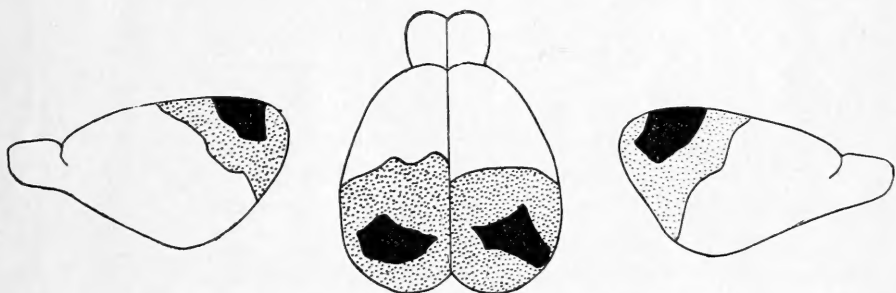

FIG. 3.—Composite diagram of the lesions in seven animals which lost the habit of visual discrimination after operation. The area which was destroyed in all is shown in solid black.

to compartments in which food is placed. At the end of each alley is a small electric bulb, 5-watt frosted "Mazda," visible from the discrimination compartment. One bulb is lighted and the other darkened in irregular alternation and the animal is trained to choose the illuminated alley, receiving food there and punishment in the darkened one. Training was continued with ten trials per day by the usual method of irregular alternation until the animals made thirty consecutive trials without entering the darkened alley. Controls were intro-

duced to assure that the reaction was to the light and not to accidental cues.

Operative methods.—Under ether anæsthesia the skull was pierced on each side of the median line at the fronto-parietal suture and the bone clipped away to make an opening, about 2 by 6 millimetres, above the caudate nucleus. Through this opening a small electric cautery, heated to redness, was plunged to a measured depth, then drawn slowly back and forth at a nearly constant depth throughout the length of the
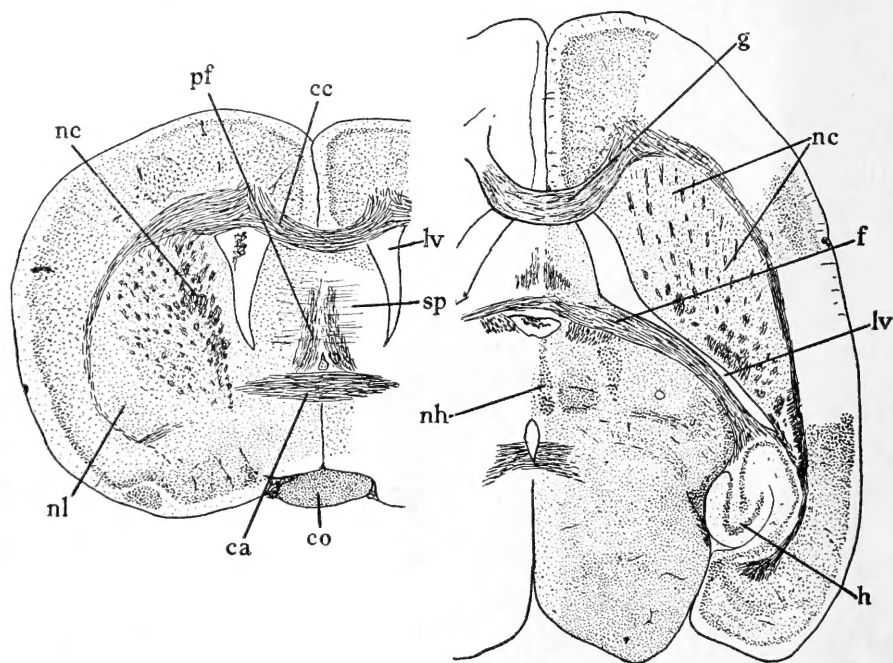

Fig. 4.—Frontal and horizontal sections through the corpus striatum at the levels of its maximum area.   *c.a.* = Commissura anterior.   *c.c.* = Corpus callosum.   *p.f.* = Columna fornicis.   *c.o.* = chiasma opticum.   *f.* = fornix.   *g.* = Genu corporis callosi.   *h.* = Lobus hippocampus.   *l.v.* = Ventriculus lateralis.   *n.c.* = Nucleus caudatus.   *n.h.* = Nucleus habenulæ.   *n.l.* = Nucleus lentiformis.   *sp.* = Septum pellucidum.

caudate nucleus. A fine scalpel was next passed from the posterior margin of the skull opening to the base of the olfactory bulb and drawn back and forth with its point in contact with the floor of the cranial cavity, so as to sever the frontal pole from the remaining cortex. In the majority of cases this method resulted in the complete destruction of the stimulable areas and in extensive lesions to both caudate nuclei. When hæmorrhage was stopped, the scalp was closed with interrupted sutures and covered with a cotton-collodion dressing.

Retention tests.—Animals trained before operation were tested in the problem box as soon as their general condition permitted; usually twenty-four hours after operation.   In these tests for retention of the habit the same method was employed as in training, except that no punishment was given for errors during the first fifty trials ; that is, the retention test is essentially a retraining in the habit and evidence for retention consists in the reappearance of accurate discrimination in significantly less time than was required for the original learning.

When a habit is lost after operation the question of post-operative shock must be considered.   In earlier papers I have discussed methods of distinguishing between loss due to shock and that due to destruction of a functional area.   In the present experiments positive evidence for retention following operation was obtained in every case, so that the question of shock does not enter, save as an explanation of the few errors made in the trials immediately following operation.

Reconstruction of lesions.—After completion of the retention tests the brains were removed and serial frontal sections stained with iron hæmatoxylin were prepared.   Camera outlines of sections at intervals of one half millimetre were made and the extent of the lesions indicated on them.   The positions of the sections were determined from internal structures and indicated on diagrams of these structures projected to the surface of the brain.   The dimensions of the lesions were then transferred with proportional dividers to the diagrams, the points so determined connected by lines and the areas inked in.   The reconstructions were finally verified by reference to the sections.

Only easily recognizable lesions, absorption or complete degeneration of the cortex and subcortical nuclei were recorded.   The diagrams, therefore, represent the minimal destruction produced by the operations. In all cases, probably, larger areas than those shown were destroyed, but, since the experiments deal with the non-function of given areas and do not seek to localize functions accurately, this fact does not invalidate the results.

Graphic and tabular presentation of results.—In the preparation of the figures a uniform system has been followed.   Diagrams of the superficial lesions made from camera outlines of an average brain are given at the top of the figure.   Below at the left is a diagram of a horizontal section through the cerebrum at the level of the maximum area of the caudate nucleus.   Practically all of the ganglion cells of that nucleus are included within the dotted line, the posterior horn being made up almost altogether of the fibres of the internal capsule.

At the right, below, is a camera outline of a frontal section through the cerebrum at the level of the anterior commissure (except in fig. 12 where the section lies at the level of the anterior horns of the lateral ventricles). In these outlines complete replacement of nervous structure by scar tissue or amorphous material is indicated in solid black; marked degeneration with some nerve elements intact is shown by stippling.

In the records of training and retention the "number of trials required for learning" represents the number of times that the animal traversed the problem box from the starting compartment to the food, before thirty consecutive trials were made without entrance into the dark alley. Ten trials were given each day in training and retention tests except where indicated. The records of these trials are given as horizontal rows of figures, each number representing the number of trials, in the ten of that day's practice, in which errors were made. Thus in the record of No. 17, 4 : 2 : 1 : 2, &c., means that on the first day four of ten trials contained errors, on the second two of ten, &c. Five errors in ten trials shows no discrimination. When no error is made for thirty trials, it is rare that errors occur in later trials unless the animal is disturbed by being roughly handled or by some new elements in the situation, such as those introduced by scrubbing the problem box.

The Formation of Habits after Destruction of the Stimulable Areas and the Caudate Nuclei.

The formation of maze, latch-box, and visual habits after destruction of the stimulable area in the rat has been reported in earlier papers [10, 12]. In the present study I have attempted to train animals after destruction of both the stimulable areas and the caudate nuclei. Only three animals have survived the operation long enough to give evidence of learning and they have formed only simple habits. The individual records of these animals follow.

No. 17.[1] Adult male.—The cautery was plunged into each caudate nucleus and the frontal pole of each hemisphere was incised. Training for visual discrimination was begun eight days after operation. For several days he spent most of the time climbing to the top of his cage and falling back to the floor. When placed in the problem box he promptly climbed out and repeated this more than two hundred times in spite of severe punishment. He

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[1] For convenience in reference these animals are numbered consecutively with others of the visual series which have been reported earlier [10, 11].

was then placed in the left-hand feeding compartment in contact with the food, and began to eat immediately.   By the process of removing him a few inches farther from the food at each trial, he was trained to find his way through the training box from the starting compartment to the food.   He was then given regular training in visual discrimination for seven days.   In this time he showed no evidence of visual discrimination, but formed a position habit toward the left alley, which was fixed in a normal learning curve, with errors (turns to the right) as follow, in successive tens of trials :—
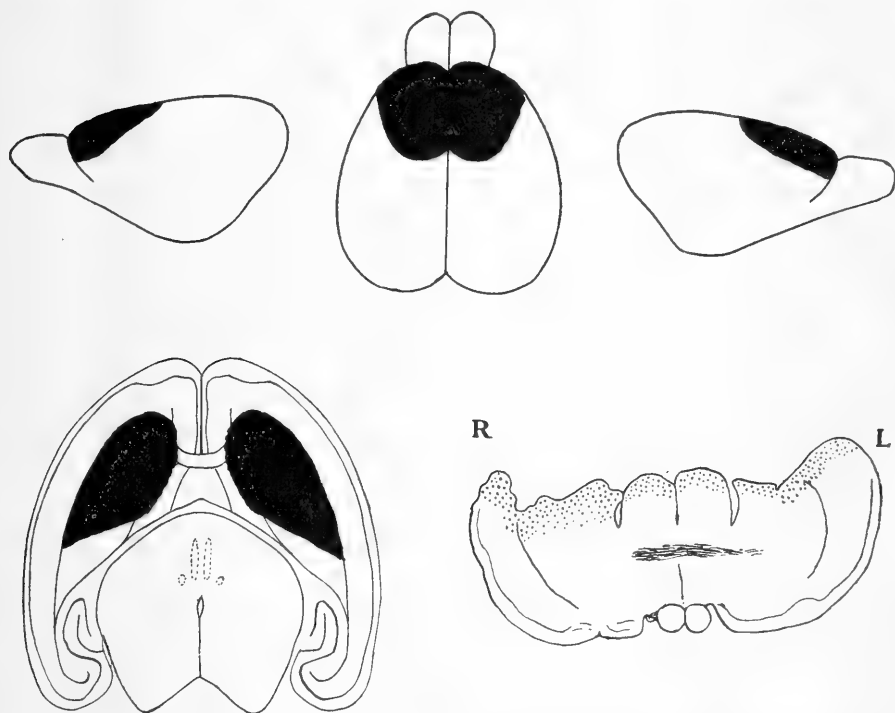
  4 : 2 : 1 : 2 : 1 : 0 : 0.

Fig. 5.—Extent of lesions in No. 17.   In this and the following diagrams a uniform arrangement has been adopted.   Above, the lesions to the cortex are shown in lateral and dorsal aspects.   Below, at the left, is a diagram of the horizontal extent of the lesions to the caudate nuclei, in this case embracing the entire extent of both nuclei.   At the right is a camera outline of a frontal section at the level of the anterior commissure, showing the depth of the lesion.   In these outlines degenerated areas are stippled and scar tissue, which does not appear in this one, is shown in solid black.   The outlines of the frontal sections are reversed, the right side appearing on the left.   The diagrams are correctly orientated.

Ten days after operation he developed a marked spasticity and died on the eleventh day.   Autopsy showed the wound infected, with extensive abscesses in both hemispheres, extending into the lateral ventricles.

Extent of lesions (fig. 5).—Right hemisphere : The entire cortex of the dorsal surface of the hemisphere, from the frontal pole to the level of the

pillars of the fornix, is replaced by a cyst. The dorsal half of the striate nucleus, including all of the caudate nucleus, is absorbed. The lenticular nucleus is uninjured. Left hemisphere: The lesion is identical with that on the right.

No. 18.   Small adult male.—The frontal lobes were transected and the caudate nuclei cauterized. For eleven days the animal showed marked disturbances of movement, rotating to the right, so that he was unable to eat without assistance. By the twelfth day this trouble had partially cleared up, so that he could walk in a straight line—although he still tended to rotate
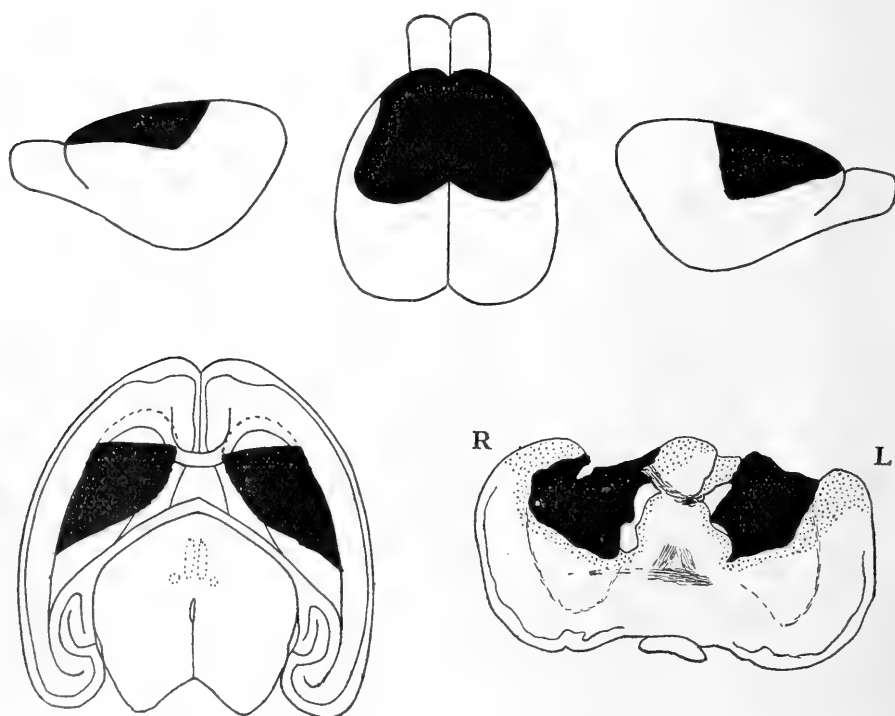

Fig. 6.— Extent of the lesions in No. 18.   Arranged as in fig. 5.

when eating. Training in visual discrimination was begun on the fourteenth day after operation. At first he had great difficulty in making the turns in the training box and in finding food, since the operation rendered him anosmic. In five days (fifty trials) he formed the somæsthetic-motor habits of the training box, so that he could go directly from the starting compartment to the food, correcting the error and orientating promptly when he failed to find food in the darkened alley. He still had some difficulty in recognizing food, and would eat shavings and fæces in the neighbourhood of the food dish, but not elsewhere. He died twenty-three days after operation.

Extent of lesions (fig. 6).—Right hemisphere. The lesion to the cortex

extends as a diagonal incision from the level of the thalamico-mamillary tract to the frontal pole, destroying all of the cortex of the dorsal convexity and extending over the superior part of the orbital surface. The caudate nucleus is completely destroyed from the level of the anterior commissure to its posterior margin. The thalamus is invaded at the level of the anterior and lateral nuclei. Left hemisphere: The lesion to the cortex is similar to that on the right, but does not extend so far laterad. The posterior part of the caudate nucleus is destroyed, as on the right. The anterior and lateral thalamic nuclei are destroyed.
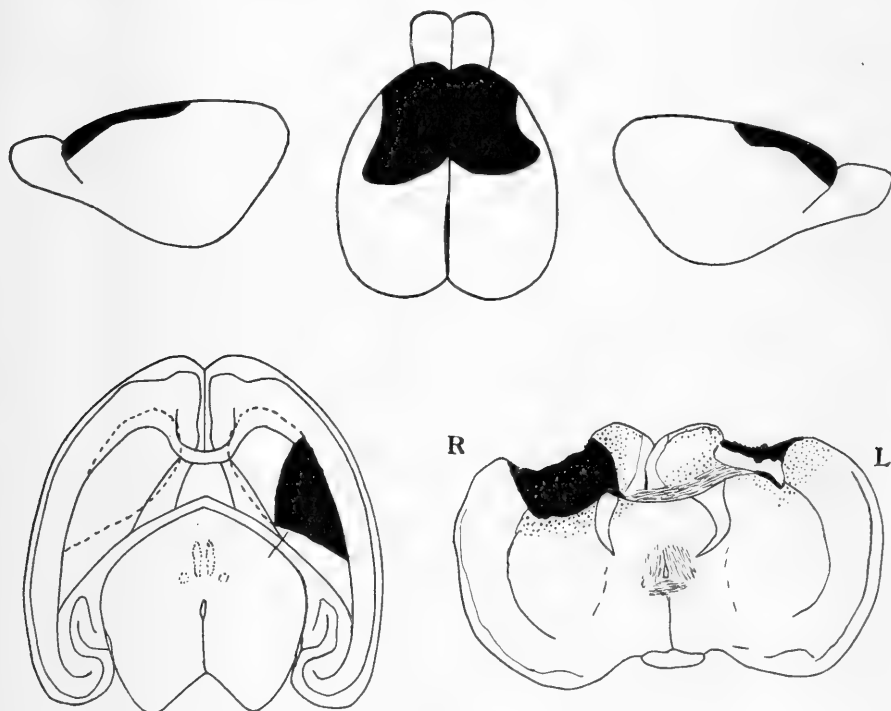

FIG. 7.—Extent of the lesions in No. 19. Arranged as in fig. 5.

No. 19. Large adult male.—The frontal lobes were transected and the caudate nuclei cauterized. Training in brightness discrimination was begun ten days after operation. The habit was formed in 130 trials with errors in successive tens of trials distributed as follows:—

6 : 6 : 2 : 5 : 5 : 2 : 1 : 3 : 1 : 1 : 0 : 1 : 1 : 0 : 0 : 0.

Extent of lesions (fig. 7).—The dorsal convexity of both hemispheres was destroyed from the level of the thalamus to the frontal pole. The orbital surfaces and olfactory tracts were not injured. The lateral portion of the right caudate nucleus was destroyed from the level of the knee of the corpus callosum to its posterior limit. The left nucleus was uninjured.

The data from these animals, in conjunction with that presented in earlier papers, establishes the fact that the rat may form somæsthetic motor habits in the absence of the stimulable cortex and of the caudate nuclei. I have shown that destruction of the stimulable area alone does not lead to an appreciable reduction in the rate of formation of visual habits, and that a difficult latch box, the " double platform box," may be learned at normal rate after complete destruction of the stimulable areas and severe injury to one or both caudate nuclei [10]. Of the three animals reported in the present study, No. 19 alone survived long enough to allow of acquirement of the visual habit and in this animal the left caudate nucleus and part of the right were uninjured. In the other two, however, the stimulable cortex was destroyed and the caudate nuclei were either destroyed, as in No. 17, or severed from their thalamic connections, as in No. 18. These animals survived only a short time, but both gave unmistakable evidence of the formation of simple somæsthetic-motor habits. From the data on the retention of visual habits after the same operation, presented in the following section, it is probable that the animals would have formed the visual habit if training could have been continued.

The problem of the relation of the extent of cerebral destruction to the complexity of the habits which may be formed must be reserved for later discussion when more adequate experimental data are available. The interest of the present study is chiefly in the question of whether or not habitual " voluntary " movements are mediated by the stimulable areas. These experiments show clearly that neither the stimulable area nor the caudate nuclei are necessary for the acquirement of such movements. This is in agreement with the results of Rothmann [16] with monkeys and justifies the conclusion that the so-called motor areas are not essential to the acquirement of voluntary activities.

This at once suggests the more important question of whether under normal conditions the motor areas are directly functional in the performance of habitual reactions. This problem has been attacked by destroying the structures after a complex habit had been acquired and testing for retention of the habit after the operation.

THE RETENTION OF VISUO-MOTOR HABITS AFTER DESTRUCTION OF THE STIMULABLE AREAS AND THE CAUDATE NUCLEI.

For tests of retention after operation the animals were trained in the discrimination box until they made thirty consecutive trials without an error. When this record was attained the problem was considered

learned, but in some cases training was continued for from 30 to 60 additional trials, as it was not always convenient to operate earlier. Since I have found that over-training up to 1,400 trials does not influence cortical localization, this additional training is not objectionable. When the problem was learned the animals were subjected to operation and their retention of the habit was tested as soon as their physical condition permitted.

In training ten trials were given daily. When the animal entered the darkened alley he was punished and the trial was recorded as an error, although he was allowed to turn back and pass through the illuminated alley to the food. In the retention tests the same method was used except that the animals were not punished. In the records given below the number of errors made in each successive ten trials of training and of the retention tests is given. Five errors are to be expected from chance if the animal is not discriminating. Fewer than four errors in ten trials suggest discrimination, and no error in thirty consecutive trials usually means that the animal will discriminate accurately thereafter. The individual records of the animals follow.

No. 20.   Large male.—Trained in visual discrimination. Sixty trials were required for learning, with errors in successive tens of trials distributed as follows :—

7 : 6 : 2 : 5 : 3 : 2 : 0 : 0 : 0 : 0 : 0 : 0.

The frontal lobes were transected and the caudate nuclei cauterized. The animal was first tested three days after the operation. He was slow and spastic, but made no error in twenty consecutive trials. For the next three days he was in an excited state and showed great fear, either refusing to run or dashing through the training box at random and paying no attention to the food. On the eighth day he was again normal in behaviour and gave clear evidence of discrimination.

Post-operative retention tests ; errors in successive tens of trials on consecutive days after operation :—

0 : 0 : (frightened, 6 : 4 : 3) 0 : 1 : 0 : 1 : 0 : 0.

Extent of lesions (fig. 8).—Right hemisphere : the lesion includes all of the cortex of the dorsal convexity from the level of the thalamus to the base of the olfactory bulb. It extends over the orbital surface at the level of the caudate nucleus where the cautery passed through the external capsule. The caudate nucleus is destroyed from the level of the anterior commissure to its posterior limit. There is some injury to the anterior thalamic nuclei. Left hemisphere : the lesion to the cortex is similar to that on the right, but does not extend on the orbital surface. The injury to the caudate and thalamic nuclei is similar to that on the right.

This animal showed unmistakable evidence of retention after

destruction of almost the entire stimulable cortex and of the posterior two-thirds of both caudate nuclei.

No. 21.   Small female about 90 days old.—Trained in visual discrimination.   Ninety trials were required for learning, with errors in successive tens of trials distributed as follows :—

8 : 5 : 5 : 3 : 2 : 3 : 0 : 4 : 1 : 0 : 0 : 0 : 1 : 1 : 0 : 0 : 0.

The frontal lobes were transected and the caudate nuclei cauterized.   For the first week after operation the animal was unable to walk except in 6-inch circles and could not make her way through the discrimination box.   By the
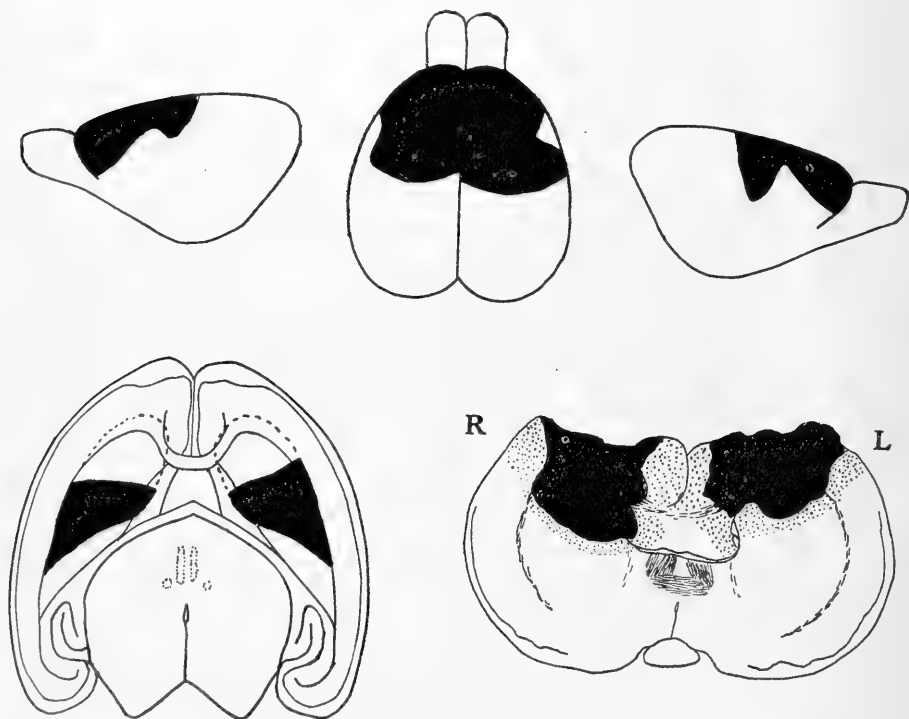

Fig. 8.—Extent of the lesions in No. 20.   Arranged as in fig. 5.

ninth day after operation the motor disturbance had cleared up so that she could walk without rotation, although she still rotated when attempting to change direction and could not turn her body to the left.   Retention tests were begun at this time and the animal at once gave certain evidence of discrimination.   The tests were continued for twelve days.   Throughout this time she was unable to turn to the left but compensated by rotating 270 degrees to the right wherever the problem box demanded a turn of 90

degrees to the left.   Fig. 14 shows some of her simpler paths in traversing the problem box.

Post-operative retention tests ; errors in successive tens of trials on consecutive days. :—

1 : 1 : 4 : 3 : 0 : 1 : 0 : 1 : 1 : 0 : 0.

Extent of lesions (fig. 9.)—All of the cortex of both hemispheres from the level of the thalamus to the base of the olfactory bulb is destroyed.   The right caudate nucleus is completely destroyed except for a small antero-medial region laterad to the forceps of the corpus callosum.   The left caudate nucleus
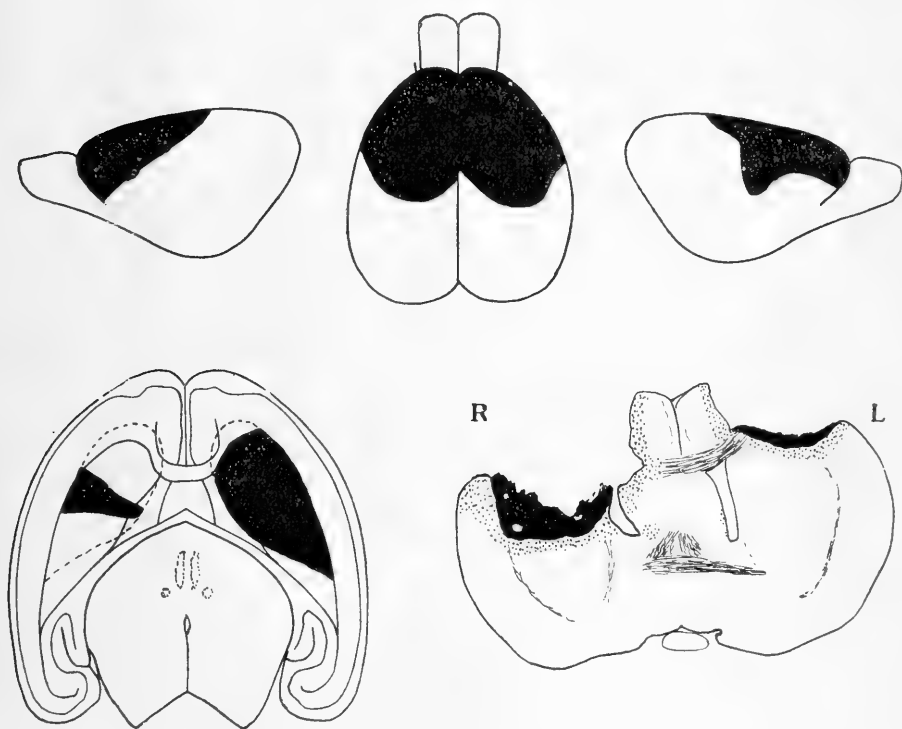

FIG. 9.—Extent of the lesions in No. 21.   Arranged as in fig. 5.

has a superficial transverse lesion at the level of the anterior commissure. The right anterior thalamic nucleus is invaded.

After destruction of the stimulable cortex and severe injury to both caudate nuclei, resulting in marked motor disorganization, this animal gave certain evidence of retention of the habit of visual discrimination.

No. 22.   Large male.—Trained in visual discrimination.   Eighty trials

were required for learning, with errors in successive tens of trials distributed as follows :—

7 : 7 : 4 : 2 : 1 : 1 : 0 : 1 : 0 : 0 : 0 : 0 : 0.

The frontal lobes were transected and the caudate nuclei cauterized. The animal was stuporous for the first day after operation, but on the second day was in fair condition and reacted promptly to the problem box, although tending to rotate to the left. On this day he made four errors in twenty trials, but the errors were obviously due to failure to compensate for the motor difficulty and his behaviour in the discrimination compartment clearly indicated discrimination. On the following and later days he made no errors.

Post-operative retention tests ; errors in successive tens of trials :—
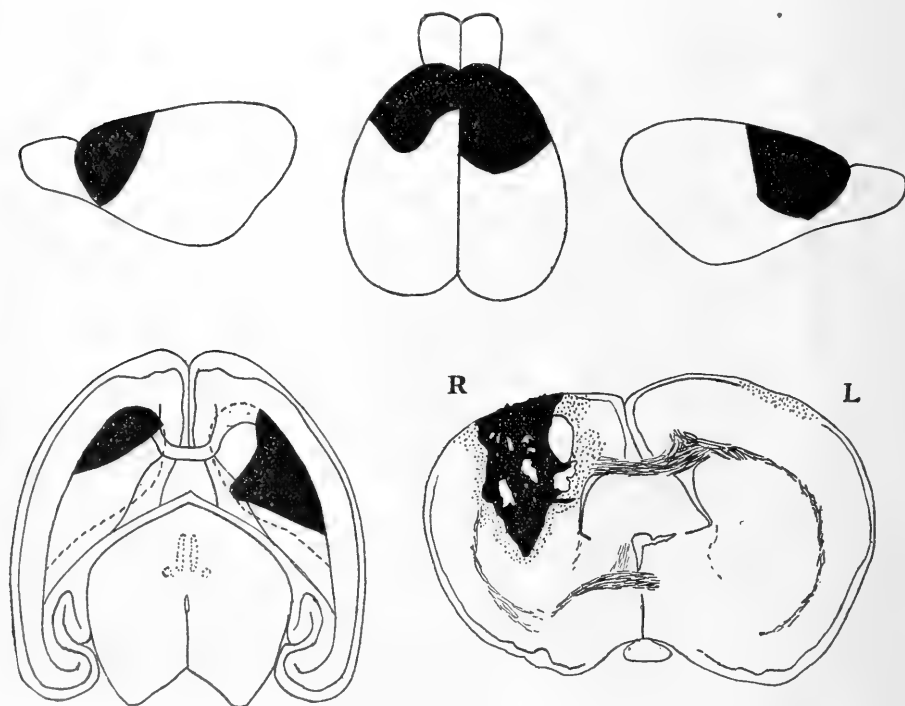
2 : 2 : 0 : 0 : 0 : 0.

FIG. 10.—Extent of the lesions in No. 22. Arranged as in fig. 5.

Extent of lesions (fig. 10).—Right hemisphere. The lesion extends from the level of the thalamus to the base of the olfactory bulb, separating all of the cortex above this plane from the underlying structures. The cortex of the orbital surface was destroyed by the cautery. The lateral portion of the caudate nucleus is destroyed by a lesion which embraces the full width of the nucleus at the level of the anterior commissure and grows narrower cephalad and caudad to this level. Left hemisphere : The incision extends

from the level of the anterior commissure to the base of the olfactory bulb, destroying all of the cortex above this plane. All of the caudate nucleus in front of the knee of the corpus callosum is degenerated ; the posterior part is uninjured.

This rat retained the visuo-motor habit after extensive but incomplete lesions to the stimulable cortex and caudate nuclei.

No. 23. Small adult male.—Trained in visual discrimination. Forty trials were required for learning, with errors in successive tens of trials distributed as follows :—

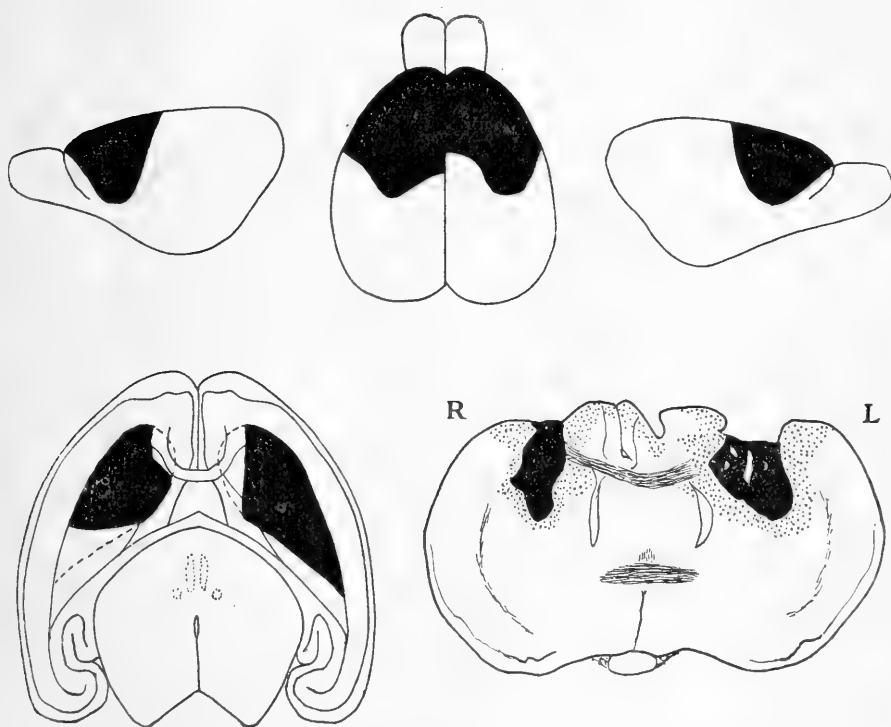7 : 5 : 2 : 4 : 0 : 0 : 0 . 0 : 0 : 0 : 0 : 2 : 0 : 0 : 0.

FIG. 11.—Extent of the lesions in No. 23.   Arranged as in fig. 5.

The frontal lobes were transected and the caudate nuclei cauterized. For three days after operation the animal's eyes were closed and he could not be tested. On the fourth day he was in good condition and gave clear evidence of discrimination.

Post-operative retention tests ; errors in successive tens of trials :—
2 : 1 : 0 : 0 : 0.

Extent of lesions (fig. 11).—Right hemisphere: The lesion to the

cortex begins at the level of the thalamus as a narrow band and broadens cephalad to include all of the cortex of the frontal pole. The lesion to the corpus striatum extends from the caudal limit of the nucleus throughout its length. All of the lateral half of the nucleus is destroyed, but the lesion probably did not involve the median part in front of the anterior commissure. The depth of the lesion is the same throughout its length, involving a little more than the dorsal third of the corpus striatum. Left hemisphere: The lesion to the cortex is practically identical with that on the right. The greater part of the caudate nucleus is destroyed, only the extreme poles remaining uninjured.

This animal showed perfect retention to the visuo-motor habit after nearly complete destruction of the motor areas.

No. 24. Small adult male.—Trained in visual discrimination. One hundred trials were required for learning with errors in successive tens of trials distributed as follows :—

4 : 5 : 3 : 5 : 1 : 3 : 4 : 0 : 2 : 2 : 0 : 0 : 0 : 0.

The frontal pole was transected and the caudate nuclei cauterized. The animal was stuporous for forty-eight hours after operation, then was tested for discrimination. He reacted slowly, but found his way through the problem box and gave some indication of discrimination, although he made frequent errors. On the fourth day of the tests he began to discriminate accurately and made no further errors.

Post-operative retention tests; errors in successive tens of trials :—

3 : 5 : 3 : 0 : 0 : 0 : 0.

The fact that the habit was reacquired in thirty trials, in contrast to the hundred of original training, shows retention rather than relearning.

Extent of lesions (fig. 12).—Right hemisphere. The lesion to the cortex begins at the level of the anterior commissure and includes all of the dorsal convexity of the frontal pole except a narrow median band. The hind leg and part of the fore leg region remain intact. All of the caudate nucleus in front of the anterior commissure is destroyed; its posterior part is uninjured. Left hemisphere: The lesion is almost identical with that on the right.

After extensive injuries to the stimulable area and destruction of the anterior halves of both caudate nuclei this animal gave evidence of retention.

No. 25. Small adult female.—Trained in visual discrimination. One hundred and ten trials were required for learning, with errors in successive tens of trials distributed as follows :—

4 · 5 · 4 : 5 : 2 : 3 : 5 : 3 : 1 : 1 : 1 : 0 : 0 : 0 : 0 : 0 : 0.

The frontal pole was transected and the caudate nuclei cauterized. For three days after operation the animal was unable to walk except in a very narrow circle to the right and could not get through the problem box. On the

fourth day she still rotated but was able to find her way through the box by keeping near the partitions, and made only one error in ten trials. On the following day she developed pronounced fear reactions and climbed out of the training box more than one hundred times. She was finally induced to make ten trials, but made six errors. Training was discontinued for five days. When she was next tested the fear had disappeared and she showed perfect discrimination.

Post-operative retention tests ; errors in successive tens of trials :—
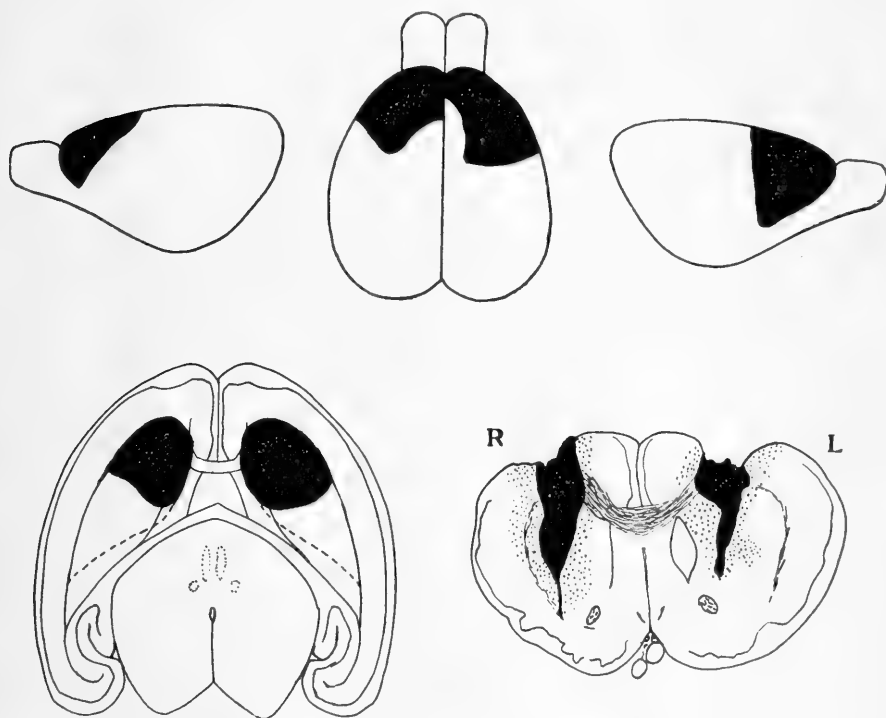1 : 6 : 0 : 1 : 0 : 0 : 0.

FIG. 12.—Extent of the lesions in No. 24.   Arranged as in fig. 5.

Extent of lesions (fig. 13).—Right hemisphere: The lesion to the cortex begins at the level of the commissura habenulæ and extends to the base of the olfactory bulb, including all of the motor cortex except a part of the hind leg area. The cautery passed throughout the length of the caudate nucleus and the entire nucleus is degenerated. Left hemisphere: The lesion to the cortex is similar to that on the right, but misses the antero-lateral surface of the frontal pole, and does not extend so far over the orbital surface. The caudate nucleus is entirely degenerated.

Practically the entire stimulable cortex and both caudate nuclei

were destroyed in this animal. There was clear evidence of retention following the operation.

This group of animals is not selected, but comprises all that survived the operation long enough to allow of retention tests. Every one of them gave evidence of retention early in the tests. Table I gives the number of trials and the number of errors, in learning and and in the post-operative retention tests. The average number of trials required for learning is eighty. Only 33·3 trials on the average
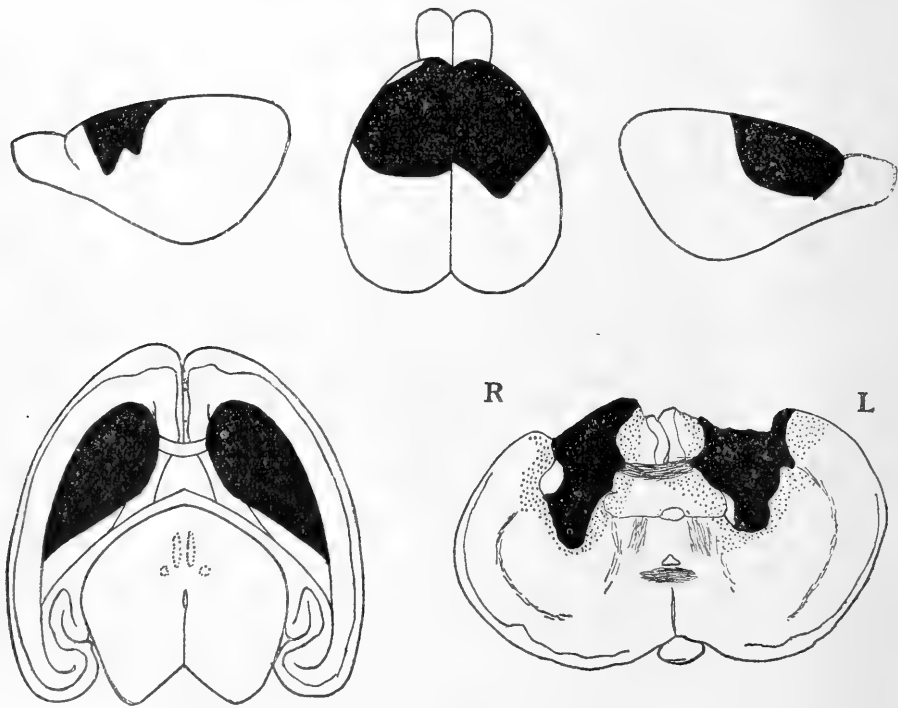

Fig. 13.—Extent of the lesions in No. 25. Arranged as in fig. 5.

were required after operation to reach the same degree of accuracy in discrimination. Errors were made in an average of 26·6 trials in learning and in only 6·3 trials in the retention tests. These figures include errors obviously due to motor disturbance and fright following operation. Thus, No. 21 was never able to turn directly to the left and all her errors seemed due to failure to compensate for the motor difficulty ; No. 24 was slow and stuporous during the time when errors were made ; six of the eight errors made by No. 25 were made

on a day when the animal was too disturbed to eat. If allowance is made for such errors, retention in every case was practically perfect.

TABLE I.—Numbers of Trials and of Errors preceding the First Thirty Consecutive Trials without Error in Learning and Post-operative Retention Tests for Animals operated after Training.

		Training			Retention tests	
		Trials	Errors		Trials	Errors
No. 20	..	60	..	25	..	0	..	0
No. 21	..	90	..	31	..	90	..	12
No. 22	..	80	..	23	..	20	..	4
No. 23	..	40	..	18	..	20	..	3
No. 24	..	100	..	29	..	30	..	11
No. 25	..	110	..	34	..	40	..	8
Average		80	..	26·6	..	33·3	..	6·3

The small operative field presented by the rat's brain and the necessity for avoiding hæmorrhage on the floor of the cranial cavity or injury to the optic nuclei of the thalamus make the complete destruction of the caudate nuclei difficult. It was accomplished only in No. 25. In this animal also the entire motor area, except the posterior part of the hind leg region, was destroyed. The animal showed motor and emotional disturbance, but gave certain evidence of retention of the habit. In No. 20 the posterior halves of both nuclei were destroyed; in No. 24, the anterior half; in the others the lesions were irregular, but even more extensive. The lesions to the cortex in all cases included the neck, fore-leg, and the greater part of the hind-leg regions.

Earlier experiments [10] had shown that no part of the stimulable cortex is necessary for the performance of the visual habit. The alternative explanations of this fact were: (1) that the striate nuclei function either vicariously for the stimulable cortex when the latter is destroyed, or normally as the source of efferent impulses from the cerebrum; or (2) that the supposedly motor regions of the cerebrum do not lie in the direct path of conditioned-reflex arcs and are of only secondary importance in the performance of voluntary movements.

The foregoing results seem to prove that the second hypothesis is correct. In the absence of the stimulable cortex, injury to the caudate nuclei does not affect retention of the visual habit and perfect discriminations may appear, even after complete destruction of both nuclei. It seems clear, therefore, that neither the stimulable cortex nor the caudate nuclei are directly functional in the performance of the visuomotor habit.

The experiments have not dealt with the lenticular nucleus and the possibility that this forms a link in the conditioned-reflex arc remains. The data previously presented on the effects of injuries to the striate nuclei [10] indicate that the caudate nucleus and the stimulable cortex together in the rat are equivalent in function to the stimulable cortex of higher forms, since their combined destruction results in relatively irrecoverable paretic symptoms. On embryological grounds there is less evidence for assuming homologous function between the lenticular nucleus and the stimulable cortex than between the latter and the caudate nucleus. In some of the earlier experiments of this series, Nos. 7 and 8 [10], the cerebral cortex and underlying association fibres were almost completely transected at the level of the anterior thalamic nuclei; in the present experiments the greater part of the internal capsule has been destroyed without abolishing visual discrimination. The cortical relations of the lenticular nucleus are not well established, but any occipito-lenticular fibres which may exist were almost certainly destroyed by these operations. It seems very improbable, therefore, that the lenticular nucleus has any more important place in the conditioned-reflex arc than has the caudate nucleus.

The evidence presented in this series of papers all points to the conclusion that in the rat the area striata on the dorsal convexity of the occipital pole is the only cerebral structure which functions in the habit of discrimination of light intensities. The habit may be formed or retained after the destruction of any other part of the cerebrum (with the possible exception of the ectorhinal and inferior temporal regions, which have not been explored but are almost certainly not functional in this habit). This means that the conditioned-reflex arcs which mediate the habit must pass to and from the cortex by way of the occipito-thalamic fibres, that the reintegrations occur within the limits of the visual area, and that long transcortical association fibres do not function in the formation or retention of the habit.

Are the conditions similar for other types of habit? There are no significant data for more complex habits. The poor vision of the rat makes the formation of complex visual habits so slow that I have not been able to carry out similar experiments with them. I have not yet located an auditory area. Certain types of latch-box habits are abolished by injury to the stimulable area [12]. The effective lesions here do not correspond in extent to the stimulable area, but only to the excitable region for the neck and fore limbs, which are used no more than the trunk and hind limbs in the manipulation of the latch. It is

probable that the loss in this case is due to the fact that the frontal region is an important somæsthetic projection area as well as electro-stimulable.   The one case for which there is clear evidence is the group of somæsthetic habits of the discrimination box which determine general orientation, finding of food, responses to doors, prompt correction of errors, &c.   These survive the destruction of any given third of the cortex [10] and of the subcortical cerebral nuclei.   It is possible that they are formed at levels below the cerebrum; it is certain that they are not dependent upon the so-called motor structures.

There is some evidence, to be reported later, that the habit of the "double platform box" [10] is disturbed but not completely abolished by destruction of either the frontal or the occipital regions.   This suggests that more complex habits involving diverse sense organs may demand co-ordination of distant portions of the cerebrum and that the visuo-motor habit dealt with in this study is too simple to give a typical picture of cerebral function.   It does not, however, indicate any greater importance of the pyramidal tracts in complex habits, and we may conclude that the existing evidence for the rat all opposes the direct participation of the "motor areas" in the performance of any habit.

The Function of the Stimulable Area and the Caudate Nucleus in the Rat.

The evidence that the stimulable cortex in the rat has no direct function in the performance of habitual motor adjustments seems conclusive.   What then is the function of this portion of the cortex?   Data for a final answer to the question are not available, but some suggestions are given by the motor disturbances following unilateral lesion to the stimulable area and the caudate nucleus.

Immediately following combined unilateral destruction of the caudate nucleus and the stimulable cortex the animal shows a very pronounced rotation toward the injured side.   Left undisturbed, he assumes a normal position, but immediately upon stimulation he bends sharply toward the side of the injury and walks in a circle, sometimes so narrow that the head is brought across the hind quarters or trips up the hind feet.   The legs of the side opposite the injury are hyper-extended and spastic (fig. 15c).   This condition may persist for several weeks, but usually clears up within a few days to such an extent that, when the animal is placed in a large open space and allowed to become orientated, he is able to walk in a straight line.   But the tendency to

rotate still appears in many situations.   When the animal is placed on
the floor he turns around several times before taking a direct course.
The necessity for avoiding an obstacle frequently results in several
complete rotations.   The tendency to rotate becomes more pronounced
in narrow quarters and in the problem box the animals have a good deal
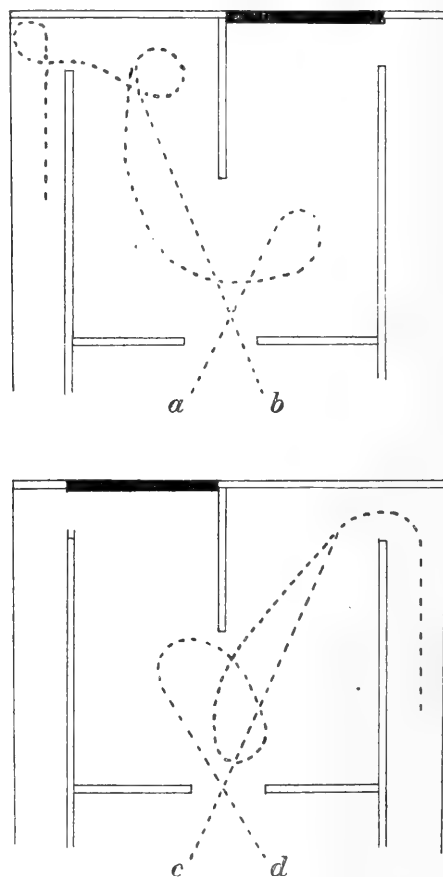

Fig. 14.—Tracings of paths followed by No. 21 in the discrimination box. The animal
was unable to turn to the left but compensated for this motor difficulty by rotation to the
right, as shown. The discrimination was in each case correct. The path varies with the
alley illuminated and with the initial orientation.

of difficulty in making the necessary turns.   Fig. 14 shows tracings of
the path of animal No. 21 at a time when she was making no errors of
discrimination.   She was able to walk in a fairly straight line, but any
need for change of direction resulted in rotation toward the right.
(Only the right caudate nucleus was injured in this animal.)   Her path

was usually more complicated than those shown, the turns involving not one but several complete rotations.
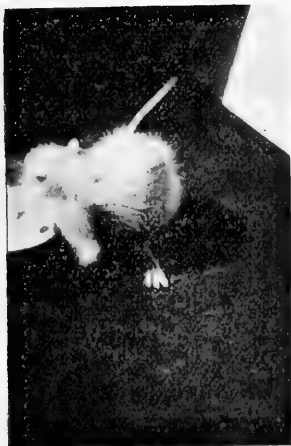
In feeding and scratching the animals show similar difficulty in

FIG. 15.—The behaviour in feeding of an animal with total destruction of the right stimulable area and caudate nucleus. For explanation see text.

adjustment. Fig. 15 shows various positions assumed by an animal with complete right unilateral destruction of the stimulable cortex and

caudate nucleus, three weeks after operation.   She approached the dish, walking in a rather wide circle, but as soon as her mouth came in contact with the food, which stimulates the normal rat to squat and assume a definite feeding position, she turned sharply to the right, the position shown at A.   She then rotated several times to the right until by chance her nose was braced against the side of the dish (B).   A similar position with hyperextension of the left legs is shown at C. Once such a feeding position has been attained it may be held for some time and a gradual relaxation of the strained posture of the body then appears.   Thus, at D, the animal was held in contact with the food for about thirty seconds, then gradually released.   She then maintained the normal feeding position for nearly a minute, turning only gradually to the right, as successive bites were taken from the edge of the cube of bread, and finally becoming overbalanced and falling.

In all the activities of such animals, the greatest disturbance of co-ordination appears when some new adjustment to the environment is necessary.   Initiation of locomotion, change in direction of locomotion, assumption of a sitting posture, stretching forward for food, scratching, &c., are attended by sudden rotations as though the difficulty were chiefly in gaining a new posture or in initiating a new activity.   Yet the activities are initiated and the disturbances are compensated for in ways that indicate that the difficulty is not at the level of the most complex integrations.   Thus, in 1917, Franz and the writer reported the case of an animal with complete destruction of the motor cortex and d egeneration of one striate nucleus, which learned the " simple maze." The maze used had essentially the same ground plan as the problem box shown in fig. 14.   The animal was trained to go constantly to the left.   He rotated and fell constantly to the right and at first could not make the turn to the left.   He finally learned to grasp the end of the partition with his left hind foot and, with this as a pivot, to swing his body to the left and so enter the food compartment.   Fig. 14 shows a more common type of adjustment where the drive toward the goal is maintained in spite of the motor difficulty.

Such adaptations seem to prove that the interference is not with the more complex integrations of voluntary reactions.   The compensations rather suggest those described by Luciani [13] for dogs after cerebellar injury, where the tendency to rotate is compensated for by walking with the body curved, and where the lesion admittedly interferes only with reflex tonic control.

The recent discussions of postural reflexes by Sherrington [17] and

Langelaan [9] and of their relation to decerebrate rigidity [Wilson, 19], suggest a possible explanation for the results of destruction of the cerebral motor structures in the rat.   The initiation of almost any new activity demands a modification of postural tone, the assumption of a different pattern of tonic contractions, which may then persist almost unaltered for some time during the performance of finer manipulative movements.   The behaviour of the operated rats suggests strongly that their chief difficulty is in taking a new posture.   Once an activity has been initiated and maintained for a moment even artificially, as when the animal is held in contact with the food, it may persist for a relatively long time until some stimulus to a new posture occurs.   The disturbances seem most pronounced in the attempts to perform those activities which require the most complex and unusual postural coordinations : scratching and feeding.   The compensations for the motor disturbances also suggest that the latter involve less complex, more nearly reflex, integrations than habitual acts.   The primary compensations are not by the direct restitution of motor control (recovery from the paresis) but by the acquisition of new patterns of co-ordination which tend to counteract the motor difficulty, much as a normal animal would adapt to a heavy weight attached to one leg.   After the destruction of the stimulable cortex the complex adaptive mechanisms are still intact.

These facts argue strongly for a relative independence of the cerebral mechanisms for control of postural activity from those for voluntary movements.   The hypothesis which seems best to fit the facts for the rat is that the stimulable area and caudate nucleus are concerned chiefly with the regulation of postural reflexes and that upon these are superimposed the more complex integrations constituting voluntary acts, transmitted to the final common paths by extrapyramidal fibres.   This would make the cerebral motor structures an additional stage in the hierarchy of spinal, vestibular, and cerebellar mechanisms for the control of postural reflexes.   Such a function has already been ascribed to the corpus striatum by Wilson [18], on the basis of work with monkeys, and the present experiments add to his conclusions only the fact that the stimulable area of the rat is to be classed in function with the striate nucleus rather than with the cerebral habit-mechanisms.

THE FUNCTION OF THE STIMULABLE CORTEX IN HIGHER MAMMALS.

Is such a view of the function of the electro-stimulable cortex contradicted by evidence from the study of higher animals ?   It is certainly

contrary to the accepted view of its function.   In current text-books of physiology and psychology it is frequently stated that the motor area is the (sole) efferent path of voluntary movements from the cortex.   Even investigators like Rothmann, who have studied recovery from hemiplegia in animals, look upon the stimulable area as the chief source of the efferent fibres concerned with habitual activity.   In speaking of conduction through extrapyramidal paths Rothmann says, " Diese extrapyramidale Leitung dürfte für die Erlernung neuer Bewegungen von grösster Bedeutung sein, während die in festen Besitz des Individuums, übergegangenen gut eingelernten Bewegungen vorwiegend die direkte Verbindung von Grosshirnrinde und Rückenmark, also die corticospinale Bahn, benutzen werden " [16].   Von Bechterew advances a similar view in describing the course of conditioned-reflex arcs across the cortex from the sensory projection areas to the motor area [1].

If this conception is correct for higher forms, it means that a pronounced change in the function of the stimulable cortex has occurred somewhere above the rodents in the evolutionary scale.   But such changes in function are rare and in this case the evidence does not seem to show more than that the stimulable cortex of higher forms has taken over a part of the function which the caudate nucleus exercises in rodents.

King [8], using the Marchi method, concluded that the pyramidal tract in the rat is small and unimportant, but Ranson [15] has shown that it is quite large, though made up chiefly of thinly medullated fibres.   The area of the tract shown on Ranson's figures is proportionally greater than in primates, so that it cannot be argued that there is any great increase in the anatomical importance of the tract with ascent in the evolutionary scale.

The physiological evidence does not seem sufficient to prove that the pyamidal tracts, even of primates, are the efferent path for impulses to voluntary movement.   Fritsch and Hitzig [5] pointed out that the paralysis following destruction of the stimulable area is only partial.   Writing of the motor centre they stated that " . . . es ist sicher, dass eine Verletzung dieses Centrum die willkürliche Bewegung des von ihm sicher in einem gewissen Abhängigkeit stehenden Gliedes nur alterirt, nicht aufhebt, dass, also irgend einem motorischen Impulse noch andere Stätten und Bahnen offen stehen um geboren zu werden und um zu den Muskeln jenes Beines zu eilen . . ."   Nothnagel observed recovery from the effects of unilateral injury to the motor area and Carville and Duret [4] first showed that the recovery is not due to

the vicarious functioning of the motor cortex of the opposite side. Rothmann [16] showed that in monkeys the extra-pyramidal paths are able to mediate learned activities. Thus it is certain that whatever the normal function of the stimulable cortex in higher mammals it is not absolutely necessary for the performance of voluntary acts.

The chief evidence for the voluntary function of the motor areas comes from the cerebral paralyses in monkeys and man. In them finer manipulative movements are greatly affected and the paralysis is much more severe than in lower mammals, yet even so it is rarely complete. The condition has been characterized as an enormous difficulty rather than an inability to move the paralysed limbs, and there is some evidence that the degree of paralysis varies with the general tonic condition of the organism.

Thus after cauterization of the stimulable cortex on one side the rhesus monkey may show a well-marked hemiplegia. But if he is badly frightened and chased about the room, he uses the limbs of both sides in an apparently normal manner. Left undisturbed, he again lapses into the paralytic condition. Gierlich [6] summarizes other examples of this sort. Similar incidents are occasionally reported for man. A girl with hemiplegia of fourteen years' standing, following diphtheria, with paralysis of the right limbs and marked contractures, tells me that when her brother pushed her from the wharf into a lake recently she used her paralysed limbs actively in climbing out. This patient is mentally retarded and perhaps not reliable. I know of no well-authenticated case of the sort, but evidence of less pronounced effects of emotional disturbance upon paralyses is frequently encountered. Depressing stimuli, such as discussion of the above patient's very distressing home conditions, increase the extent of contracture and limit the power of voluntary movement. Exciting stimuli, on the other hand, will sometimes increase the extent of voluntary movement, and have been used to advantage in re-education (personal communication from Dr. S. I. Franz).

All these facts point to the conclusion that, even in primates, it is not so much the mechanism of voluntary movement which is affected in cerebral paralysis, as some facilitating mechanism whose action is usually essential to the movement, yet is not a part of the direct conditioned-reflex arc. Graham Brown's study of facilitation after section of the connections between pre- and post-rolandic areas [3] shows that the descending fibres from both areas act upon the same final common paths, and that transcortical connections are not necessary for the mutual

facilitation of the areas. Voluntary movements are possible in the absence of the motor areas; there is not conclusive evidence that they function directly in habit; the phenomena of cerebral paralysis can be explained on the assumption that the motor area is postural and facilitating in function; there is clear evidence that the analogous structures in lower forms are not directly concerned with the performance of learned activities. Although not conclusive, these considerations seem sufficient to cast doubt upon the accepted explanation of the function of the motor cortex, and to demand further experimental investigation before we can conclude that the pyramidal tracts form the efferent path for impulses to voluntary movements.

SUMMARY.

It has been shown that the albino rat is able to acquire somæsthetic-motor habits after destruction of the electro-stimulable cortex and the caudate nucleus. Visuo-motor and simple somæsthetic-motor habits which are acquired before the operation are retained after the destruction of these structures and probably after the section of occipito-lenticular fibres. It is clear, therefore, that neither the cerebral-motor areas nor the subcortical nuclei are directly concerned with the performance of learned activities.

Combined destruction of the motor area and the caudate nucleus results in relatively permanent motor disturbances resembling hemiplegia in monkeys. Evidence is given that the difficulty is primarily in assuming new attitudes, and it is suggested that the primary func tion of the cerebral motor structures in the rat is the regulation of postural reflexes. Existing evidence does not seem to exclude such an explanation of the function of the stimulable cortex, even in man.

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A PSYCHOLOGICAL INQUIRY INTO THE NATURE OF THE CONDITION KNOWN AS CONGENITAL WORD-BLINDNESS.

BY LUCY G. FILDES.

THE aim of the investigation about to be described was to discover something of the psychological characteristics of the condition commonly called by the misleading term of congenital word-blindness—a condition which shows itself most clearly in the subjects' extreme difficulty, or even total failure, in learning to read, and appears to be closely related to the various forms of acquired alexia met with commonly as the result of brain injury in later life.

Three explanatory theories, it will be remembered, have been put forward as indicating the nature and cause of this condition, viz. :—

(1) A theory which assumes the existence of definitely localized and circumscribed visual and auditory word-centres in the brain, the destruction or isolation of which will destroy language in either its visual or its auditory aspect ;

(2) A theory which interprets word-blindness as only one symptom in a general lowering of mental ability ; and

(3) One which attributes the condition to a more specialized lowering of power in the primary visual centres, rendering true visual perception of words and of other complex sense-data difficult.

The main problems raised by these different interpretations are two in number. Is inability to learn to read or the loss of the power of reading due to specific or to general defect? If the former, does the defect show itself only in reading, or does there appear to be any general lowering of visual power? A psychological investigation should throw light on these points.

The subjects mainly used for the investigation were twenty-six in number—all children between the ages of 9 and 16 years, who were in attendance either at ordinary elementary schools (4) or at special schools for mentally defective children (22). They were selected on the report of their teachers as finding reading a very great difficulty. Before the work peculiar to the investigation was begun, all the children were tested (a) with the Stanford revision of the Binet scale, in order to get